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ECOLOGY, BIOGEOGRAPHY, AND CONSERVATION OF COASTAL PLAIN PLANTS: SOME GENERAL PRINCIPLES FROM THE STUDY OF NOVA SCOTIAN WETLANDS

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ABSTRACT

The existence of a coastal plain flora in southwestern Nova Scotia was first documented by Fernald in the 1920's. Recent field work has documented the distributions of coastal plain species more accurately, and there is now a growing emphasis on research dealing with habitat conservation.

Most Atlantic coastal plain plants in Nova Scotia are confined to infertile sand and gravel shorelines on lakeshores where fluctuating water levels prevent shrubs from colonizing the broad, open shorelines. The species are also abundant where exposure to waves is intense. On such shorelines, wave action reduces soil fertility by washing away small soil particles and organic matter. Coastal plain species are very tolerant of such nutrient-poor conditions and can be considered "stress-tolerators." The plants are not abundant at fertile sites apparently because they cannot successfully compete against tall, fast-growing species that normally occur on fertile soil. As a result, the small, slow growing coastal plain plants are restricted to sparsely vegetated shorelines.

Increasing numbers of these species are receiving recognized status from the Nature Conservancy and from the Committee on the Status of Endangered Wildlife in Canada. In spite of this, existing habitat continues to be threatened by cottage development and the use of all-terrain vehicles. The establishment of a conservation strategy to preserve what remains of the flora should include 1) the preservation of whole habitats, 2) consideration of global status of the species, and 3) the incorporation of reserves, buffer zones, and community education and participation.

Key Words: Coastal plain flora, conservation priorities, water level fluctuations, wave exposure, infertility, stress-tolerator, all-terrain vehicles, seed bank

INTRODUCTION

Our knowledge of the distribution and ecology of coastal plain plants falls neatly into two eras. The first began with the pioneering work of Fernald (1921, 1922) in documenting the existence of these species in Nova Scotia, and ended with the synthesis provided in the Flora of Nova Scotia (Roland and Smith, 1969). These and intervening studies established firmly that southwestern Nova Scotia was botanically distinct from the rest of Canada. A second series of coastal plain communities were documented

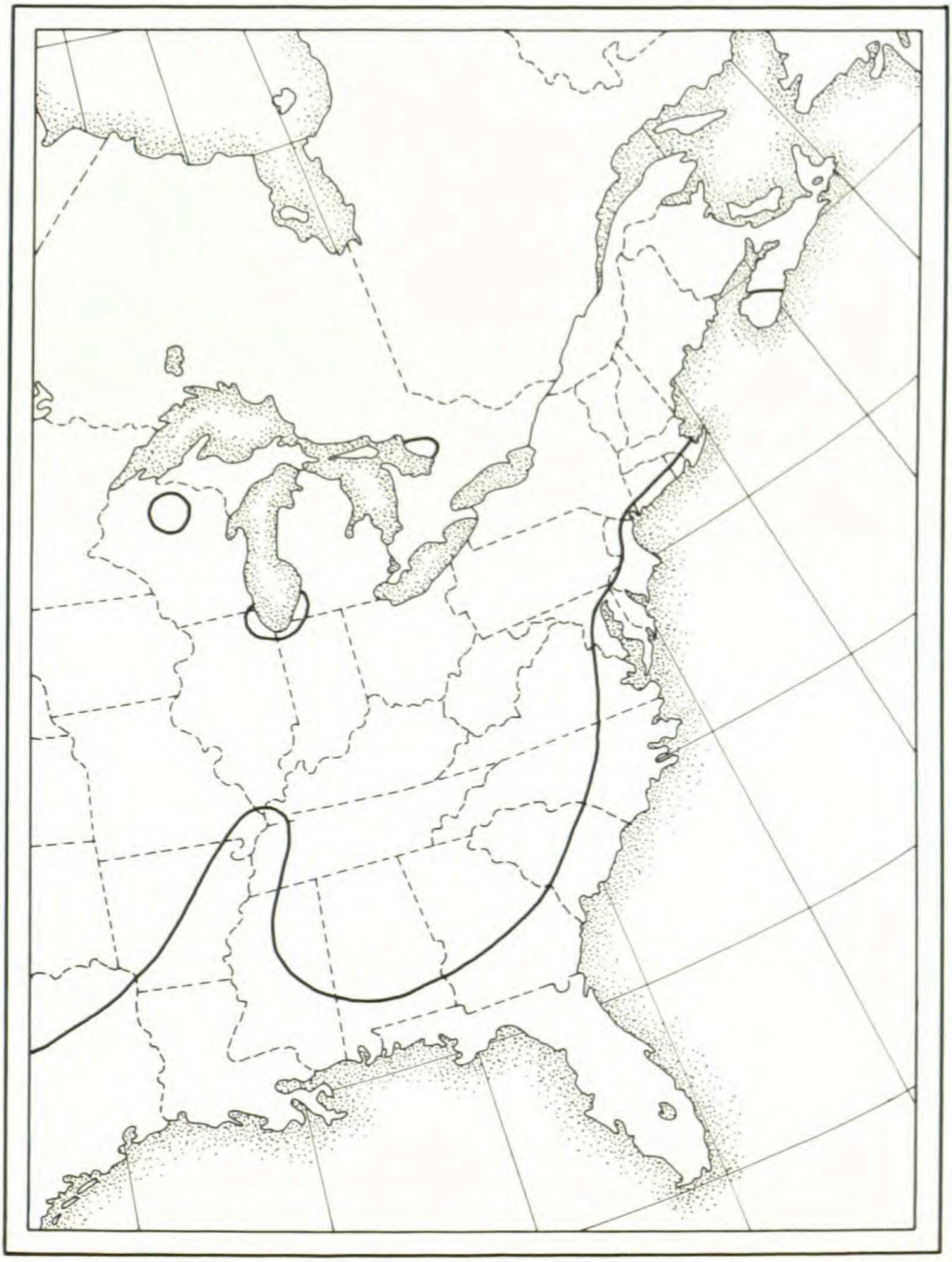

Figure 1. Distribution of Atlantic coastal plain species.

in Canada in the Great Lakes Watershed in the early 1980's (Figure 1; Keddy and Reznicek, 1982; Keddy and Sharp, 1988).

Simultaneously, the second era in our knowledge of coastal plain species began. Emphasis shifted from floristics to ecology and conservation (Keddy, 1985a, 1985b; Wisheu, 1987; Wisheu and Keddy, 1989a). The principal objective of this paper is to review, using published and previously unpublished data, what we have learned about the ecology and conservation of Atlantic coastal plain floras in the past decade. Although the major emphasis will be upon southwestern Nova Scotia, the region can be thought of as a model system for other coastal plain wetlands.

BIOGEOGRAPHY

Coastal plain species are believed to have spread to Nova Scotia about 14,000 years ago after the retreat of the Wisconsin glaciation (Roland, unpubl.). The world sea level at that time was over 100 m below the present level and both Browns and Georges Banks were exposed (Figure 2). It is thought that by migrating across this land bridge, species were able to spread northward from the Cape Cod region to Nova Scotia.

The flora occurs within the warmest area of the province, the southwestern edge, with 160–180 frost free days each year (National Atlas of Canada, 1981). Coastal plain species seem restricted by cold temperatures because their numbers diminish as one moves progressively northward (Gleason and Cronquist, 1964). The southwestern region of Nova Scotia is also overlain by sedimentary, rather than metamorphic rock (Figure 3) and it is within the regions of greywacke that the flora is most abundant (Figure 4).

The distributions of coastal plain species within southwestern Nova Scotia follow three patterns. Firstly, there are those species that are relatively widespread, such as *Ilex glabra, Woodwardia areolata, Panicum longifolium,* and *Solidago galetorum* (Figure 4a). They occur throughout the warm region, primarily in the areas with greywacke. A second group of species has a more restricted distribution, but a distribution without an obvious pattern. *Lachnanthes tinctoria,* for example, occurs at only one lake, although it is quite common there. *Clethra alnifolia* is known from only two unconnected lakes and is absent from similar lakes that are nearby. The distribution of *Lophiola americana* also lacks an obvious pattern (Figure 4b). The disjunct nature of this latter group of species suggests that the populations are remnants of once more widespread vegetation (Roland, unpubl.). Since the species are at the northern extentions of their ranges, they may no longer be capable of sexual reproduction, and may therefore be incapable of reestablishing extirpated populations.

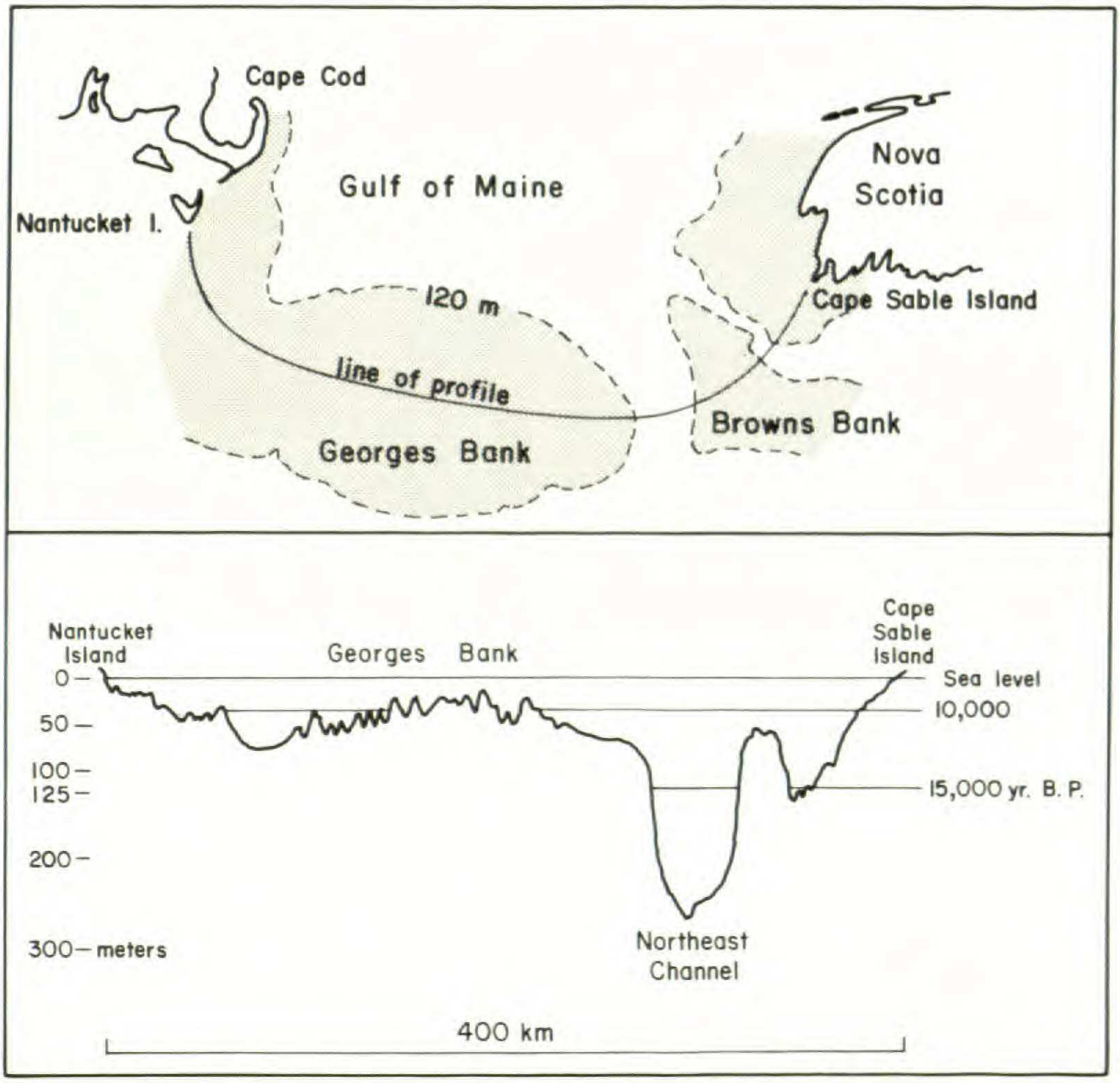

Figure 2. Changes in sea level in relation to a profile from Nantucket Island, Massachusetts, to Cape Sable Island, Nova Scotia (after Ogden and Harvey, 1975).

A third group of species is again quite restricted in distribution, but there is a discernable pattern. Species such as *Coreopsis rosea* and *Sabatia kennedyana* (Figure 4c) are restricted to the Tusket River Valley in Yarmouth County (Keddy, 1985a). These species may be restricted to this one watershed because of their poor dispersal ability or because only in this region are appropriate physical conditions found. Transplant experiments may reveal whether it is dispersal limitations or availability of suitable habitat which produces these patterns.

ECOLOGY

An initial description of the coastal plain flora concluded that in Nova Scotia, the species are found, almost without exception,

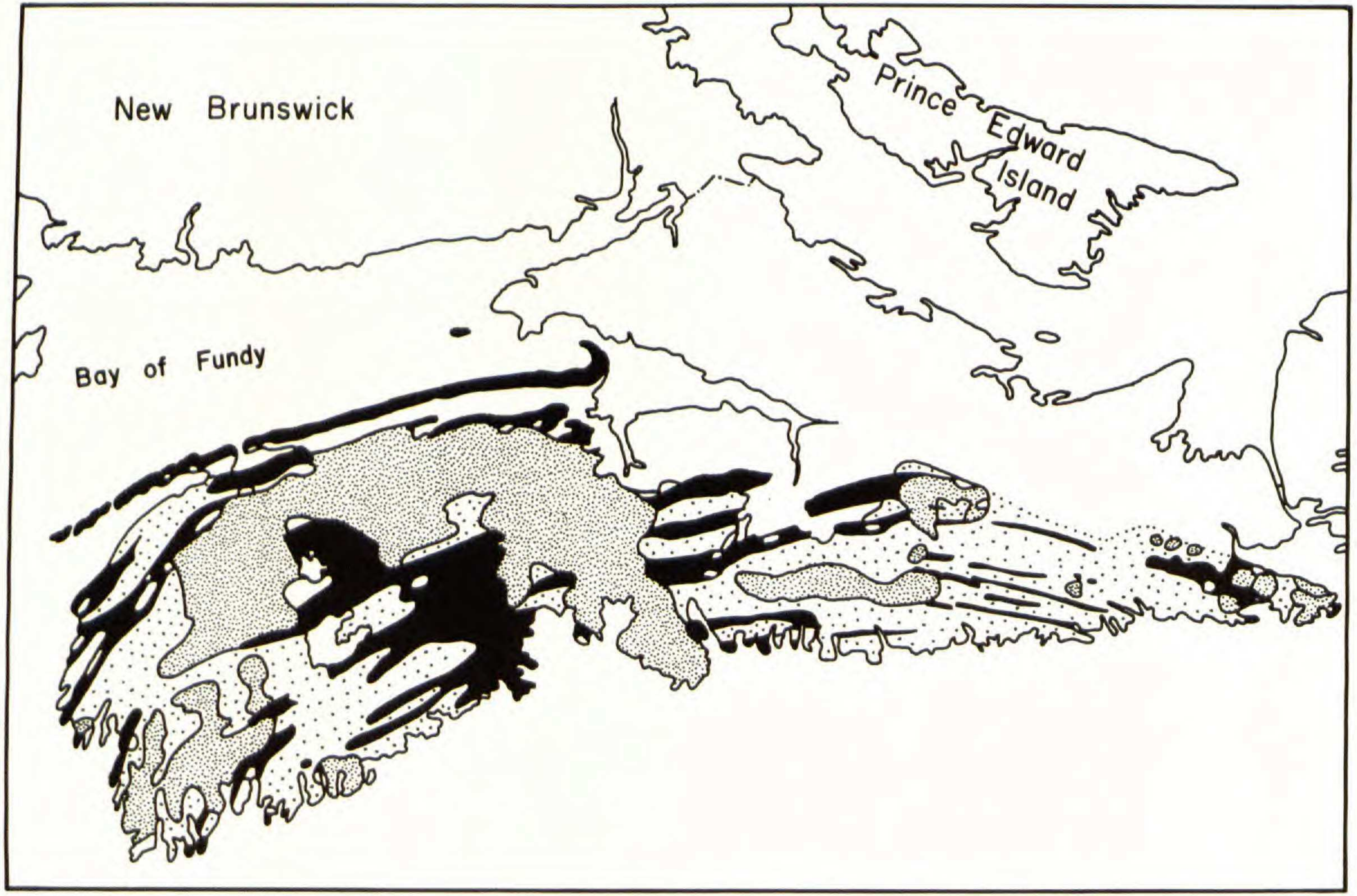

Figure 3. Some rock types found in southwestern Nova Scotia. Slate and North Mountain basalt areas are in black, granite areas are heavily stippled, and greywacke areas are lightly stippled (after Roland, 1982).

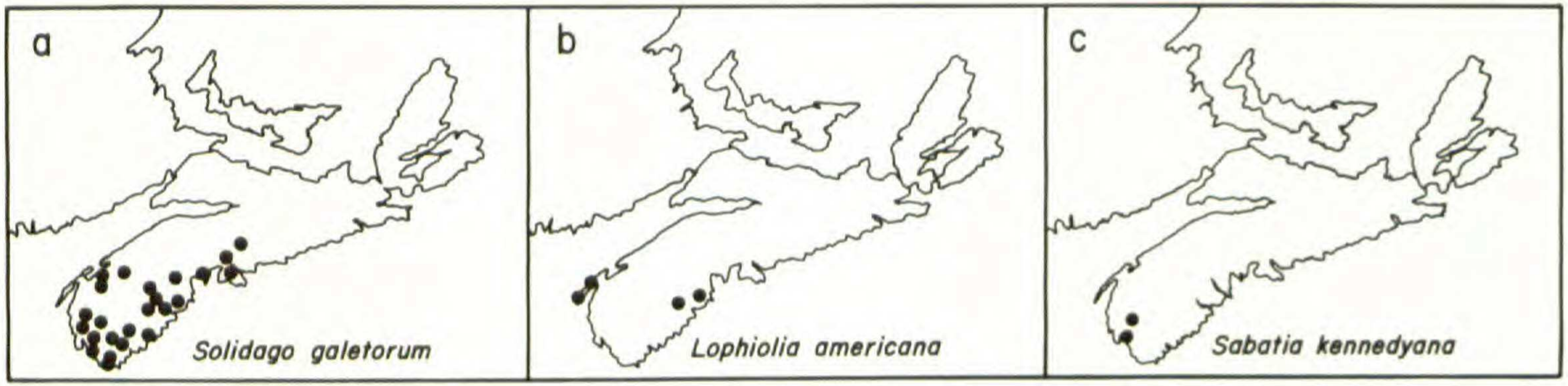

Figure 4. Distributions of selected species in Nova Scotia (after Roland and Smith, 1969).

Table 1. Abundances of Atlantic coastal plain species on lakeshores of different substrate types within the same lake (Wisheu, 1987). Coastal plain species are as in Roland and Smith (1969).

	Red Till	Local Till
No. of species	52	57
No. of coastal plain species	8	9
Contribution of coastal plain species to species richness (%)	15.4	15.8
Contribution of coastal plain species to above ground biomass (%)	23.8	9.5

in moist or wet freshwater areas (Roland, unpubl.). We have since learned much more about the distributions of these plants and we can now begin to predict at which lakes and where on each lake coastal plain species may be found.

Among Lake Distributions

As a result of a complex geological history (Grant, 1977, 1980), lakes in southwestern Nova Scotia are of a variety of shapes and sizes and are typically situated on one of two glacial tills. The first till, called "local till" (Grant, 1977), consists of large angular boulders and produces steeply sloping boulder lakeshores. The second "red till" is made up of smooth gravels. It is on the broad, gently sloping shorelines of "red till" that coastal plain species are most abundant (Table 1).

The coastal plain flora is most abundant in lakes which experience large water level fluctuations, such as Kejimkujik Lake (Keddy, 1984a; Roland, unpubl.), Ponhook Lake (Keddy and Wisheu, pers. obs.), and the lakes of the Tusket River system (Keddy, 1985a). Coastal plain plants have been shown to be associated with fluctuating water levels in Ontario as well (Keddy, 1981; Keddy and Reznicek, 1982).

In lakes with frequent fluctuations in water level, shrub growth is inhibited and shorelines remain broad and open (Keddy and Reznicek, 1982, 1986; Keddy, 1985a). Shrubs exclude herbaceous coastal plain species (Keddy, 1983; Sharp and Keddy, 1985). When water level fluctuations are infrequent, shrubs are killed when high water levels return and the herbaceous community has a chance to reestablish from the seed bank. Coastal plain species

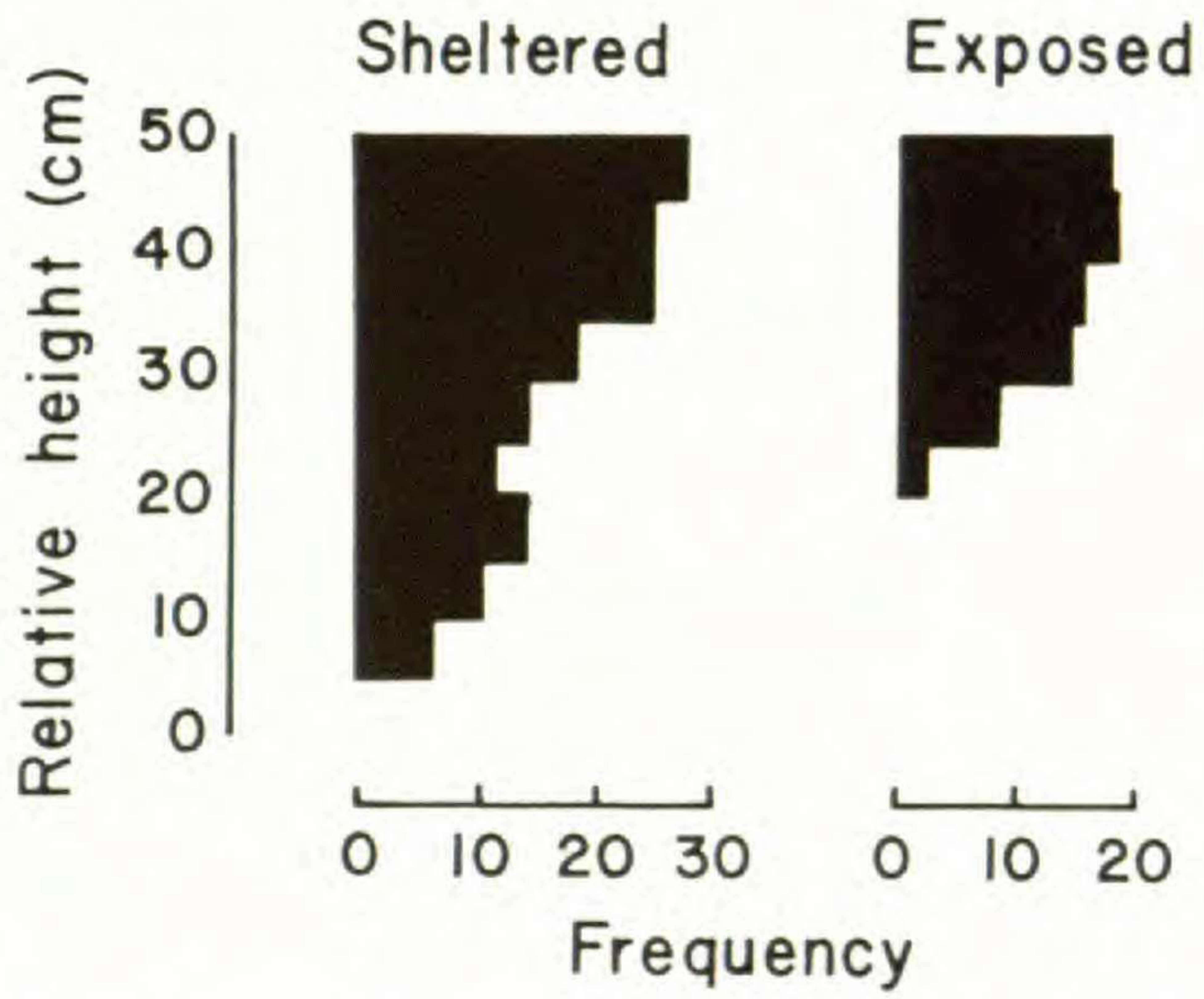

Figure 5. The position of the lower limits of shrubs on exposed and sheltered lakeshores plotted as frequency of shrub species at each elevation summed over ten transects on each shore type. Shrubs occurred more frequently and closer to the water level on sheltered than on exposed shores (after Keddy, 1983).

in Ontario and New Jersey persist in this manner (Keddy and Reznicek, 1982; Nicholson and Keddy, 1983; McCarthy, 1987; Keddy et al., 1989).

The broad, open shorelines suitable for coastal plain plants are also produced by wave exposure. Wave action has two effects. Firstly, at wave-exposed sites, shrubs are prevented from crowding out herbaceous species (Figure 5). Large lakes can therefore support coastal plain species because their exposed shorelines are kept free of shrubs by waves. Waves also inhibit the formation of bogs, a shoreline community in which few coastal plain plants are found (Keddy, 1981).

The second effect of exposure to waves is that the fertility of shorelines is reduced. Wave energy is inversely proportional to organic content (Keddy, 1985b), silt and clay content (Keddy, 1982, 1984b, 1985b), and concentrations of P, K, Mg, and Ca (Keddy, 1985b). The association of coastal plain species with infertile conditions is also indicated by the large number of insectivorous species that grow alongside the coastal plain plants (Moore et al., 1989; Wisheu and Keddy, 1989a, 1989b). The coastal plain species on the New Jersey pine barrens are also growing in soil with low fertility (Gleason and Cronquist, 1964).

Within Lake Distributions

Since conditions vary along lakeshores, coastal plain plants are not equally abundant on shores even within a single lake. For example, coastal plain plants are most abundant within a zone that is below the shrub line where flooding is frequent (Figure 6). Water depth is a factor known to be important to all shoreline plants (Hutchinson, 1975; Spence, 1982). Other factors that determine the within lake distribution of the species include those which determine among lake distributions: till type and exposure.

On lakes where shorelines include different substrate types, coastal plain species are best represented on the broad, gently sloping "red till" shores (Keddy, 1984b; Wisheu, 1987; Wisheu and Keddy, 1989a). When wave action varies along lake shorelines, the flora is most abundant where exposure is greater (Figure 7). There, the elimination of shrubs and the reduction of fertility create ideal coastal plain habitat.

The effects of infertility and ice and wave disturbance on plant communities can be summarized by a model first proposed by Grime (1973, 1979; Figure 8). This model shows that in areas where stresses (infertility) and disturbances (exposure) are minimal, standing crop and litter is high. Species richness, however, is low in such areas since a few tall, fast-growing species suppress all others. These dominant species lose their competitive superiority in regions which are moderately stressed or disturbed (Grime, 1973, 1979), with the result that maximum species richness occurs in areas of moderate standing crop and litter (Figure 8a). In areas with extreme levels of stress or disturbance, only a few species are able to tolerate the physical environment and both species richness and standing crop and litter are low. It is in these regions of low standing crop and litter than the coastal plain flora is most abundant (Figure 8b; Wisheu, 1987; Moore et al., 1989; Wisheu and Keddy, 1989a).

The mechanisms which restrict species to exposed shores have

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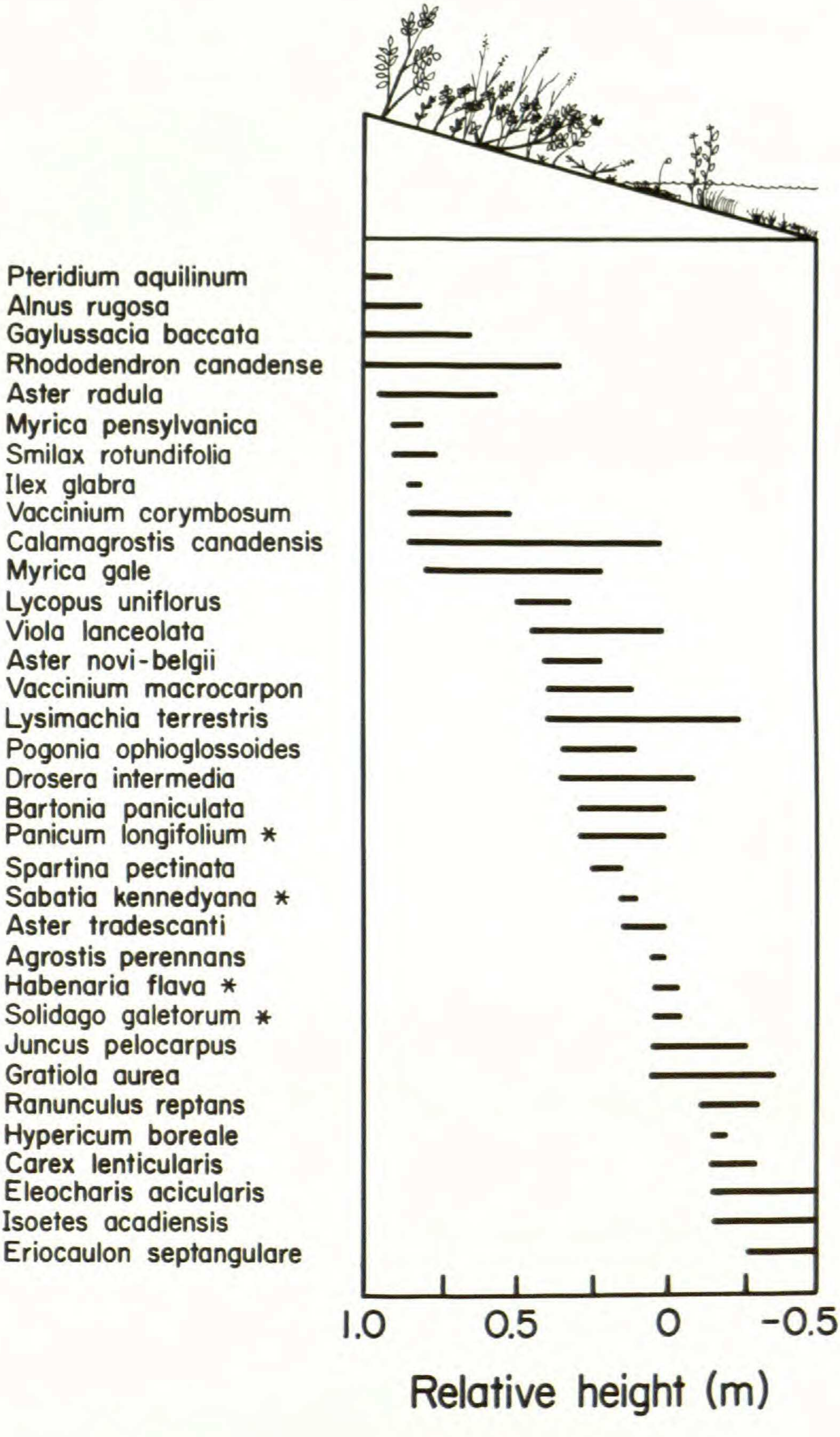
Figure 6. Transect of a typical shoreline on the eastern side of Gillfillan Lake, Nova Scotia (Keddy, 1984a). Asterisks indicate species that are nationally significant (*see* Table 2). (Reproduced with permission from the British Ecological Society.)


Pteridium aquilinum
Alnus rugosa
Gaylussacia baccata
Rhododendron canadense
Aster radula
Myrica pensylvanica
Smilax rotundifolia
Ilex glabra
Vaccinium corymbosum
Calamagrostis canadensis
Myrica gale
Lycopus uniflorus
Viola lanceolata
Aster novi-belgii
Vaccinium macrocarpon
Lysimachia terrestris
Pogonia ophioglossoides
Drosera intermedia
Bartonia paniculata
Panicum longifolium *
Spartina pectinata
Sabatia kennedyana *
Aster tradescanti
Agrostis perennans
Habenaria flava *
Solidago galetorum *
Juncus pelocarpus
Gratiola aurea
Ranunculus reptans
Hypericum boreale
Carex lenticularis
Eleocharis acicularis
Isoetes acadiensis
Eriocaulon septangulare
1.0
0.5
0
-0.5
Relative height (m)

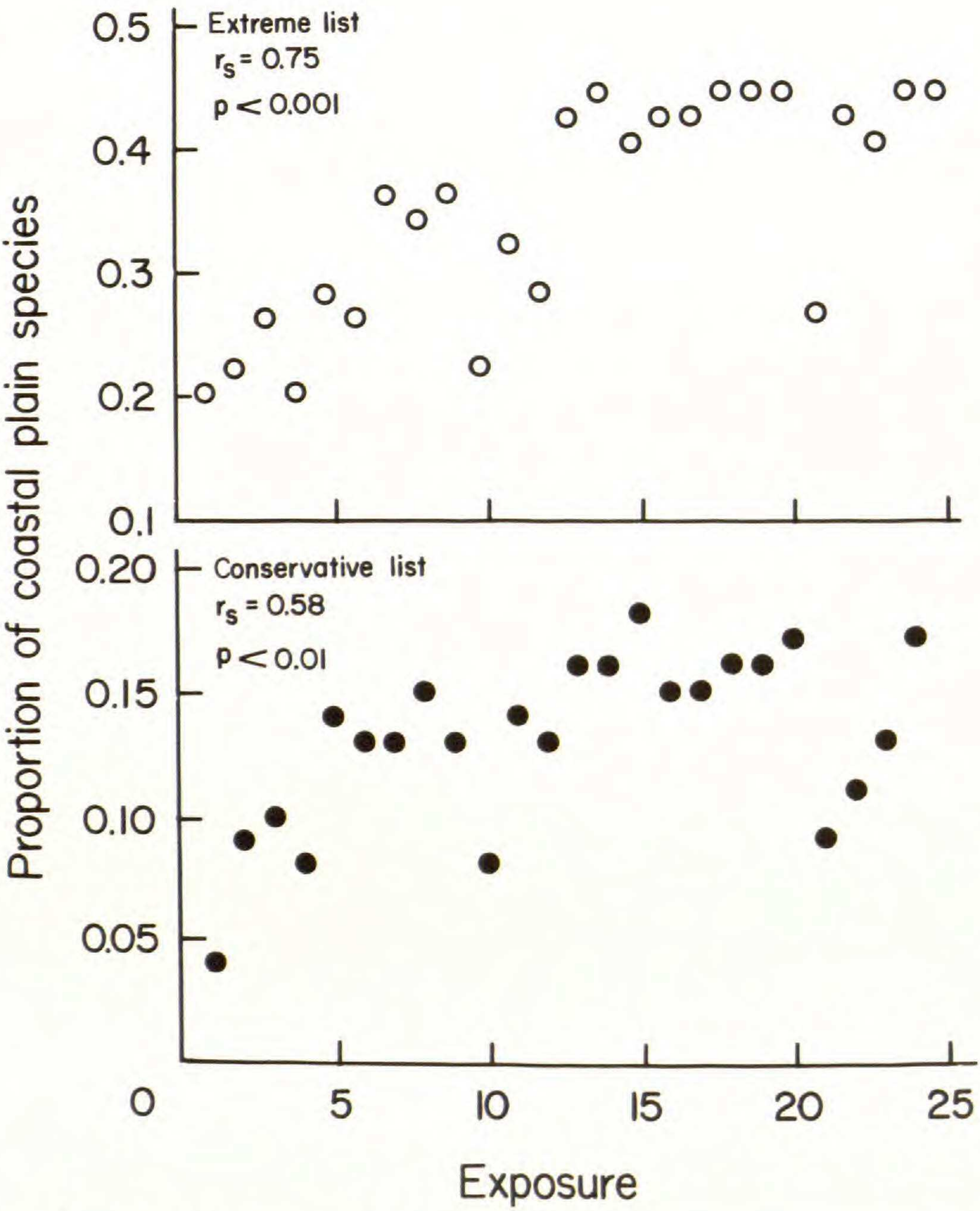


Figure 7. The proportion of Atlantic coastal plain species along an exposure gradient in Axe Lake, Ontario. The conservative list of coastal plain species consists of *Rhexia virginica, Juncus militaris, Nymphoides cordata, Utricularia purpurea, U. resupinata,* and *Xyris difformis*. The extreme list includes *Cladium mariscoides, Drosera intermedia, Juncus pelocarpus, Myriophyllum tenellum, Muhlenbergia uniflora, Potamogeton confervoides, P. oakesianus, U. cornuta,* and *Viola lanceolata*. Nomenclature follows Gleason and Cronquist (1963) except for *Xyris difformis* Chapman. "r_s" indicates the Spearman rank correlation coefficient (Keddy, 1985b). (Reproduced with permission from the *Canadian Journal of Botany*.)

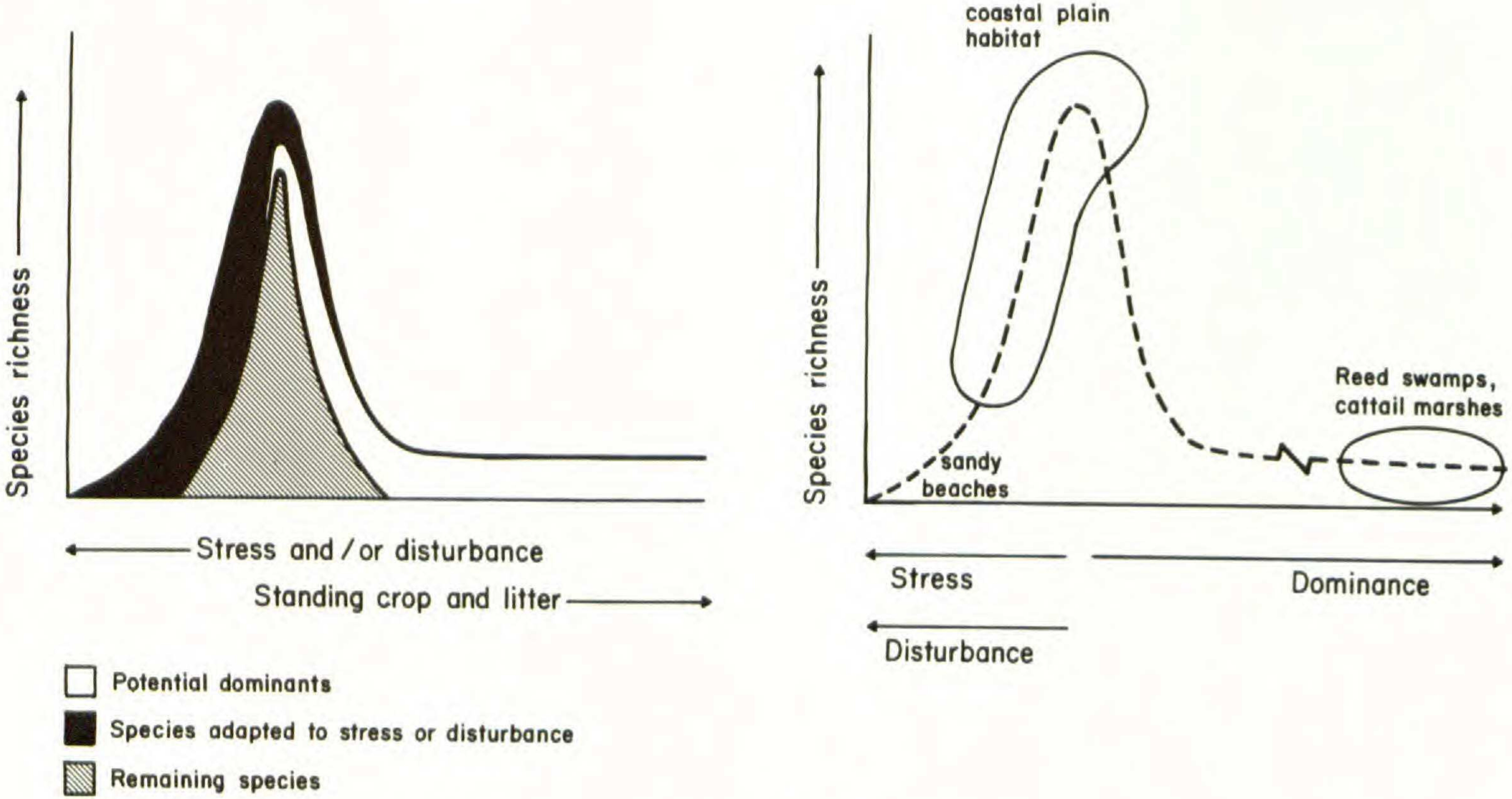


Figure 8. Model summarizing the effect of stress and disturbance on species richness, species distributions, and standing crop and litter. The left figure is from Grime (1973, 1979) and the right relates it to our current understanding of shorelines and coastal plain habitat.

been the object of extensive experimental studies. Wilson and Keddy (1985) recreated the lakeshore soil gradient in pots and showed that species with different field distributions tended to all show best growth in substrate from sheltered bays, suggesting that these species had inclusive niche structure or "shared preferences" along this gradient. A transplant experiment lasting two growing seasons (Wilson and Keddy, 1988) showed that both survival and growth rates decreased with increasing exposure. Grime (1973, 1977, 1979) predicted that stress-tolerators were poor competitors, and more recent experiments confirm this. Wilson and Keddy (1986a) showed that competition intensity increased from infertile beaches to sheltered bays. Moreover, those species with the weakest competitive ability were restricted to infertile beaches (Wilson and Keddy, 1986b)—the habitat with the lowest competition intensity. Gaudet and Keddy (1988) screened forty-four wetland plant species for competitive ability and found that the small partially evergreen species were, in general, poor competitors. The two coastal plain species in the experiment (*Sabatia kennedyana* and *Panicum longifolium*) both had weak competitive ability relative to other more widespread shoreline species (e.g., *Lythrum salicaria, Bidens cernua,* and *Typha latifolia*). This accumulated evidence suggests that coastal plain species occupy habitats which strong competitors cannot invade.

Many members of the coastal plain flora occupying these habitats are small, slow-growing species with rosette growth forms and with evergreen tissue (Wisheu, 1987, 1989b). These traits are associated with the stress-tolerator strategy (Grime, 1977); Greenslade (1983) and Southwood (1988) call such species "adversity selected." Their growth form is similar to the "isoetid" (Hutchinson, 1975), a group of aquatic species considered to be "stress-tolerators" (Boston, 1986; Boston and Adams, 1987; Wisheu and Keddy, 1989a, 1989b). The similarity of coastal plain species to isoetids also shows up in their distributions along the standing crop gradient (Figure 9).

Superimposed upon the effect of standing crop is the effect of peat accumulation. Our field observations suggest that on wave exposed shorelines, a cyclical succession occurs: vegetation cover increases in large stands of *Cladium mariscoides* and then declines when the *C. mariscoides* is eroded away (Figure 10). In recently scoured or disturbed areas, species such as *Lobelia dortmanna* and *Hydrocotyle umbellata* occur on the exposed sand and gravel

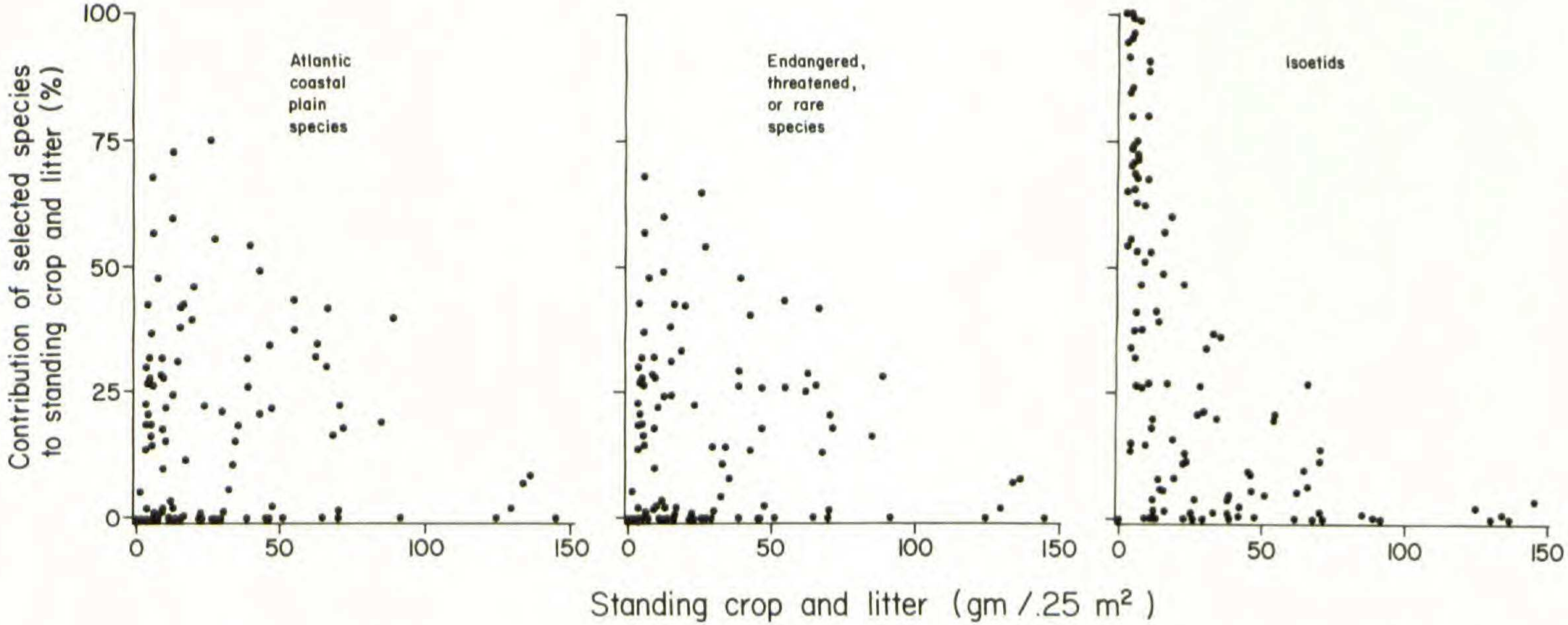


Figure 9. Contribution of selected species to standing crop and litter as plotted along a standing crop and litter gradient at Wilsons Lake, Nova Scotia (Wisheu and Keddy, 1989a). (Reproduced with permission from Elsevier Applied Science Publishers.)

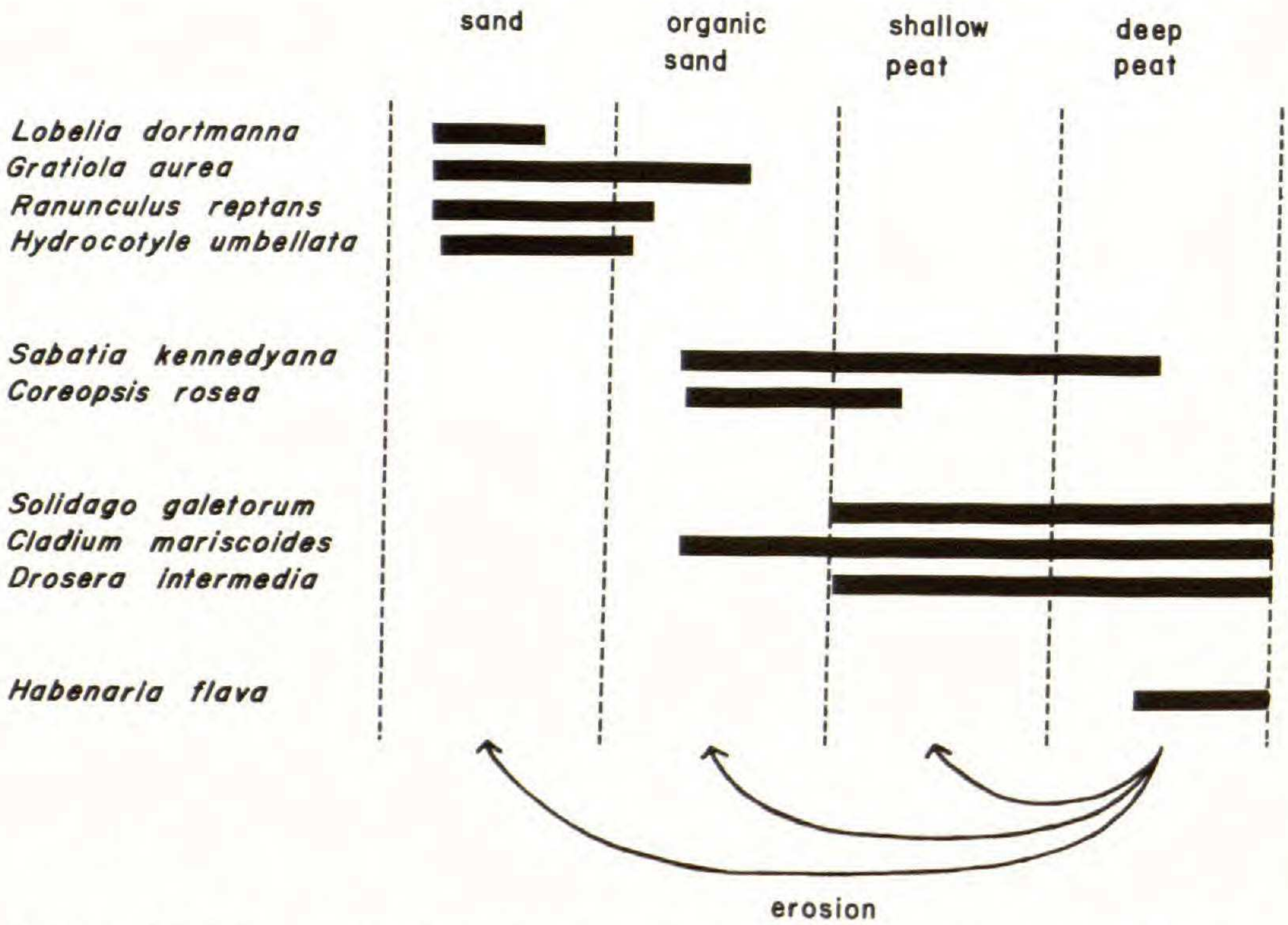


Figure 10. Apparent dynamics of vegetation on exposed shorelines. The establishment of *Cladium mariscoides* and peat accumulation are associated with increasing plant cover and changes in species composition. Erosion (arrows) reverses the process. When peat is eroded and washed up on the shoreline, it is colonized by species such as *Rhexia virginica, Panicum longifolium, Carex folliculata, Vaccinium macrocarpon, Aster nemoralis, Juncus filiformis,* and *Myrica gale.*

substrate. Where some organic material or silt is present, *Sabatia kennedyana* and *Coreopsis rosea* also occur. Once *C. mariscoides* has established and formed a shallow peat layer over the sand and gravel substrate, *Drosera intermedia, S. kennedyana, Solidago galetorum,* and *Lycopodium inundatum* increase in abundance. As peat accumulates to a depth of several centimeters, species such as *Habenaria flava* invade. Inevitably, disturbance removes the peat layer and restores the shoreline to a sand and gravel substrate. Species such as *Panicum longifolium* and *Rhexia virginica* are often found where this eroded peat has been pushed up on the shore. The exposed beaches therefore appear to have green islands of *C. mariscoides* invading gravel in some areas and being eroded away in others. A similar process appears to occur in Ontario where both *C. mariscoides* and *Rhynchospora fusca* apparently initiate succession.

CONSERVATION

Since coastal plain species are restricted to a specific habitat within a limited geographical area, it is not surprising that many members of the flora are either endangered, threatened, or rare. Loss of habitat in both Canada and in the United States has reduced populations of some of the species to the point where the species are now threatened globally (Table 2).

If existing populations of coastal plain species are to persist, then in the long run, the stresses and disturbances that are maintaining the populations must be maintained. Stabilizing water levels, for example, would encourage shrub growth which could eliminate the coastal plain species (Keddy and Reznicek, 1982). Constant water levels would also eliminate the regeneration of the species from the seed bank (Keddy and Reznicek, 1982, 1986; McCarthy, 1987). Nutrient enrichment of the infertile shores through logging or agricultural runoff would also adversely affect the flora by encouraging the development of common, more competitive species. Such a change has already occurred in the New Jersey Pine Barrens where development has enriched sections of the barrens, sections that now have fewer rare species than pristine regions (Ehrenfeld, 1983; Morgan and Philipp, 1986).

While habitat management must be an essential part of a long term conservation strategy for these species, the greatest present threat to the coastal plain flora is simply the destruction of suitable habitat. Populations of coastal plain species on several lakes in the Tusket River system were destroyed when the lakes were turned into reservoirs by a hydroelectric dam (Keddy, 1985a). Cabin development and the associated landscaping of lakeshores (including contouring by bulldozers) have also destroyed large tracts of shoreline both in Nova Scotia (Keddy, 1985a) and in Cape Cod (B. Sorrie, pers. comm.).

All-terrain vehicles, however, are the most immediate threat to the flora. The gently sloping gravel shorelines which support the flora are ideal areas for driving the vehicles. The frequent passage of all-terrain vehicles has already destroyed 90% of what was once one of Canada's largest stands of *Sabatia kennedyana* (Wisheu and Keddy, 1989a). Damage by all-terrain vehicles may destroy not only the established vegetation, but the seed bank as well. The soil of a heavily damaged site had only 550 viable seeds/m^2 as compared to an intact shoreline with 10,000 viable seeds/m^2 (Keddy et al., 1989; Wisheu and Keddy, unpubl.).

Table 2. The Canadian, American, and global status of selected Atlantic coastal plain species.[1]

Species	Status			
			U.S.A. (no. of states)	
	Global	Canada	Extant	Extirp.
Bartonia virginica	5	*	29 (5)	
Clethra alnifolia	5	**	21 (1)	
Coreopsis rosea	3	***	7 (4)	3
Glyceria obtusa	5		13 (1)	
Habenaria flava	4?	*	17 (6)	
Hydrocotyle umbellata	5	***	26 (2)	
Ilex glabra	5		17 (2)	1
Lacnanthes tinctoria	4	*	16 (6)	
Lophiola americana	3–4	**	9	
Lycopodium inundatum bigelovii	5		25 (6)	1
Panicum dichotomiflorum	5		45	
Panicum longifolium	?	*	19 (3)	3
Panicum spretum	?		25 (1)	1
Polygonum hydropiperoides	5		47 (2)	
Rhexia virginica	5	*	32 (4)	
Rhynchospora capitellata	5		34	
Sabatia kennedyana	3	**	4 (4)	
Sisyrinchium atlanticum	5		27 (5)	1
Smilax rotundifolia	5		30	
Solidago elliottii ascendens	3?		7 (5)	1
Solidago galetorum	?	*		
Utricularia radiata	4	*	21 (4)	1
Utricularia resupinata	4?		15 (6)	2
Utricularia subulata	5	*	19 (5)	
Woodwardia areolata	5	*	27 (5)	2
Xyris difformis difformis	5?	*	23 (3)	1

[1] Canadian status is from Argus and Pryer (unpubl., * rare) and the Committee on the Status of Endangered Wildlife in Canada (** threatened, *** endangered). American and global rankings are from Kartesz (unpubl.) and The Nature Conservancy (1987, scale from 5 (demonstrably secure) to 1 (critically imperiled)). The figure in parentheses is the number of states which have assigned the species a rank of 3 or less. Nomenclature follows Roland and Smith (1969) except for *Xyris difformis* Chapman var. *difformis*. Coastal plain species are those listed by Roland and Smith (1969) with the addition of *Rhexia virginica* and *Utricularia resupinata*.

There are four reasons why coastal plain species may be particularly sensitive to disturbance from all-terrain vehicles. Firstly, some coastal plain species such as *Sabatia kennedyana* are evergreen, and the loss of leaf tissue from evergreen plants not only reduces the plants' ability to photosynthesize, but may also seriously reduce the nutrient capital of these plants which are growing in impoverished soil. Secondly, rates of recovery after a disturbance (as measured by biomass accumulation) appear to be lower along exposed shores than along sheltered shores (Sharp and Keddy, 1985). Long recovery times in such habitats would mean that relatively infrequent disturbance from all-terrain vehicles could have major impacts upon the vegetation. Third, the evidence from growth form suggests that in addition to slow growth imposed by the habitat, these species may have inherently slow growth rates, further reducing their recovery rates after disturbance. Lastly, common ruderal species such as *Juncus* spp. are most abundant in the seed bank (Figure 11; Keddy et al., 1989; Wisheu and Keddy, unpubl.). The creation of gaps within a coastal plain community would therefore allow common genera to gradually replace the rare flora if disturbance from all-terrain vehicles continues.

Threats to the coastal plain flora are both numerous and widespread so it is imperative that we act quickly to preserve what remains. Disjunct populations are at particular risk because once extirpated, there are no immediately adjacent plants that can recolonize (Reznicek, 1989). Also, protecting whole habitats as a general conservation strategy increases the probability that the protected system will be self-perpetuating and more resistant to the occasional perturbation. This same strategy also maximizes efficiency by allowing many species to be protected at once. The establishment of Nova Scotia's first nature reserve in the Tusket River system protected not one, but eight significant species. Careful selection of future reserves can further multiply the number of species that are secure in at least one region.

Local priorities, however, must not be the only criteria with which to select new reserves and new target species. One must consider status in other regions. *Clethra alnifolia,* for example, has the same Canadian rank (threatened) as *Sabatia kennedyana*; yet *C. alnifolia* is common in the United States (Table 2) while *S. kennedyana* occurs in only four states, all four of which consider it rare. An ecological reserve, then, to protect *C. alnifolia* would be a lower global priority than a reserve to protect a population of *S. kennedyana.* There is a clear need to look beyond provincial or national boundaries when establishing conservation priorities.

The long term maintenance of the landscape and watershed

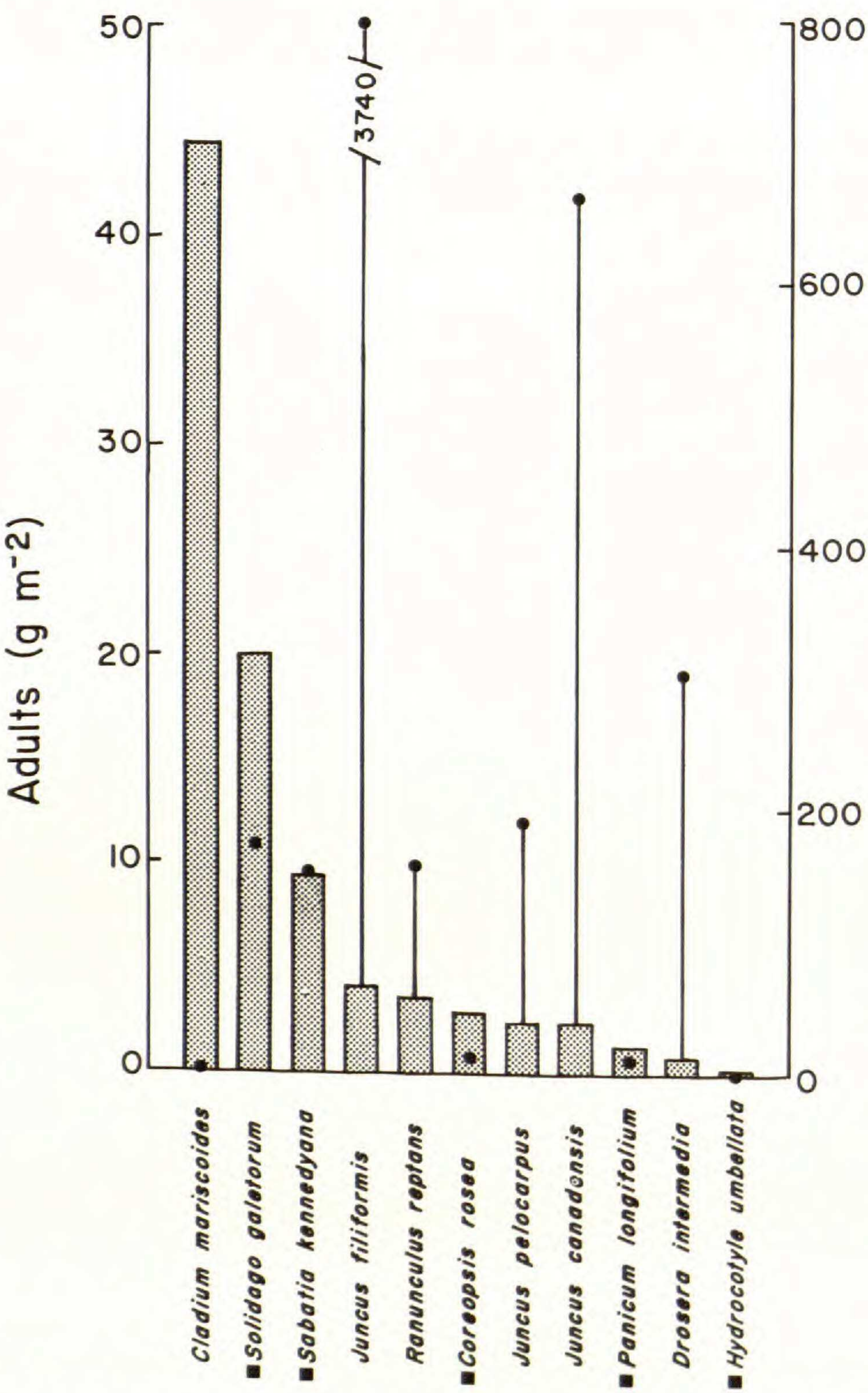


Figure 11. Occurrences of selected species as adults and as germinable seeds in the seed bank at Wilsons Lake, Nova Scotia. Coastal plain species are indicated with solid squares (Keddy et al., 1989). (Reproduced with permission from Academic Press, Inc.)

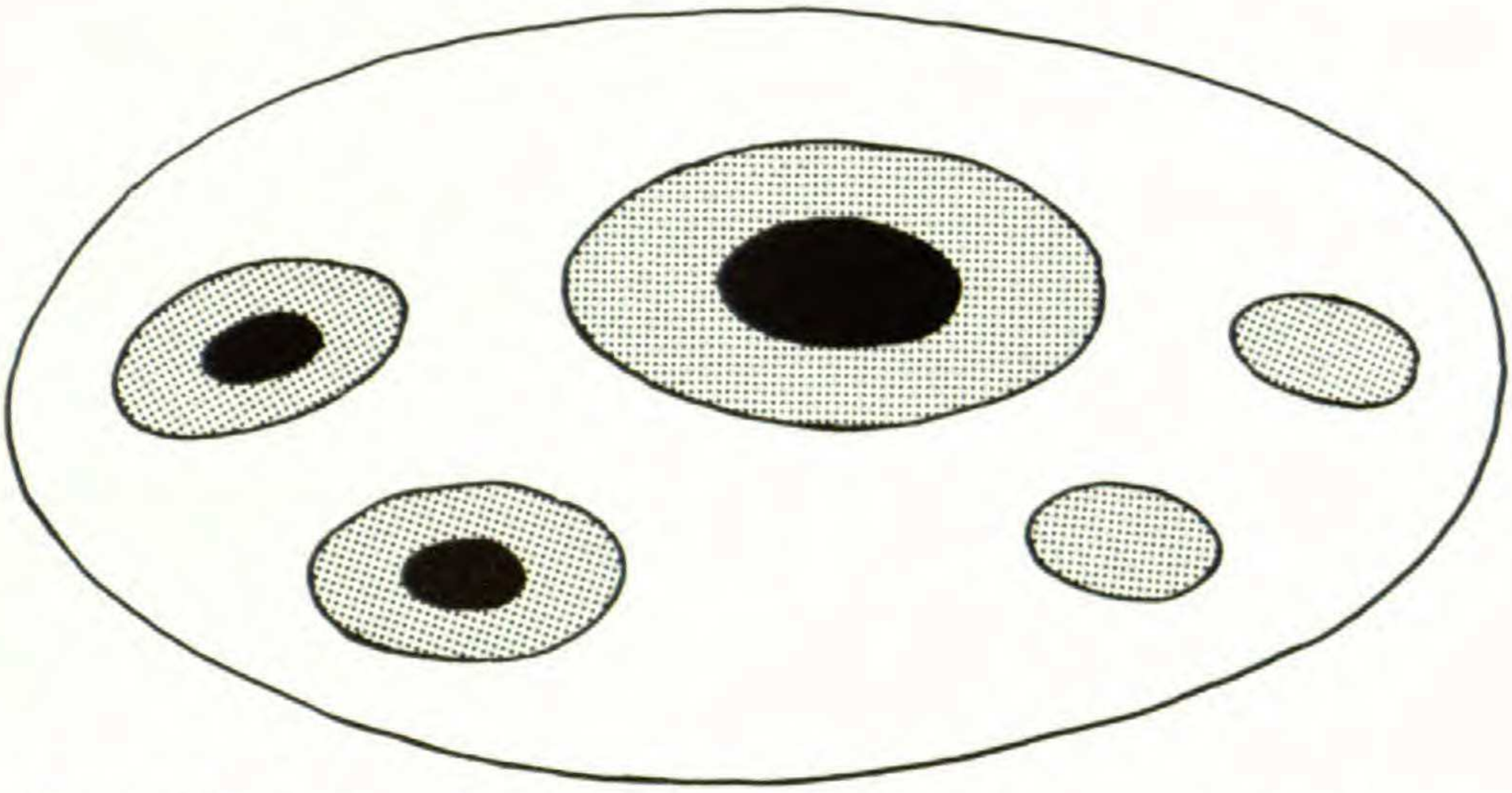


Figure 12. An integrated reserve system: reserves are shown in black, buffer zones are stippled, and the management area with educated and concerned landowners is white. The scale of the diagram can vary from a watershed to an entire state.

around reserves is also essential. The selection of target species and the establishment of new reserves should be followed by a public relations campaign aimed at educating local landowners. Brochures and exhibitions could modify land use activities that are detrimental to the reserve and its flora. People could be taught, for example, to keep all-terrain vehicles off lakeshores. An educated public would also facilitate the establishment of buffer zones around reserves. Fewer people would oppose the zones while educated landowners would be more willing to act as land stewards. Finally, an educated public could minimize the need for more reserves. The Nova Scotia museum is now actively involved in such a program.

The long term goal, then, of plant conservation should be a reserve system that integrates reserves into the surrounding landscape (Figure 12; *see* Katz, 1986, for example). Buffer zones around reserves that are surrounded by educated, concerned residents will not only protect the target species but will also preserve a variety of other vegetation types. The ultimate objective of such a system should not only be to keep a list of species present, but to represent the range of vegetation types and array of natural communities in which they occur.

In conclusion, our knowledge of biogeography and ecology of coastal plain species has increased significantly over the past decades. But this knowledge must be used to guide a more aggressive, long term conservation strategy for coastal plain plants in North America as a whole. Points to consider when designing such a strategy include 1) preserving whole habitats, 2) considering the global status of species, and 3) establishing conservation plans that incorporate reserves, buffer zones, and community education and participation.

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